Invited Paper

Interactions of Parasitoids and Checkerspot Caterpillars *Euphydryas* spp. (Nymphalidae)

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Abstract. *Euphydryas phaeton* caterpillars have a variety of escape and defensive behaviors. These behaviors vary among instars. The caterpillars can effectively ward off *Apanteles euphydryidis* wasps. These parasitoids exhibit varying attack behaviors relative to the different prediapause instars of *E. phaeton*. Comparison of *A. euphydryidis* and *Benjaminia euphydryadis* suggests that these wasps employ alternative strategies for larval parasitism of the same host. The host-parasitoid interactions described here reflect the spatial and temporal availability of the caterpillars to their insect enemies. The availability of early instar larvae spatially (at webs) varies dramatically, with periods of few larvae alternating with periods of abundant hosts.

    Climatic factors affect the temporal availability of *Euphydryas* species to their parasitoids, especially *Apanteles* species with multiple generations per that of the host. Hence, parasitism was not a major factor in most population fluctuations of *Euphydryas* species, either among localities or years at sites. Other aggregated host-parasitoid systems are expected to parallel the patterns shown here, with parasitoids responding to host patches in terms of numbers of available hosts and exhibiting various search and attack behaviors depending on the changing behavior of the hosts.

Introduction

Ecological and behavioral studies of lepidopteran hosts and parasitoids interacting in natural populations are rare (Matthews, 1974; Morrison & Strong, 1980). Yet to understand how and when parasitoids are able to subdue host populations to observed or desired levels, it is necessary to determine the availability of hosts spatially and temporally relative to their parasitoids under natural conditions. In host-parasitoid systems where the caterpillars are gregarious, parasitoids may be drawn in numbers to these host patches. Consequently, interactions between the caterpillars and parasitoids may be more readily observed and correlated with population responses of the hosts and parasitoids than in systems where the hosts are solitary.

The first objective of this review is to examine Baltimore checkerspot caterpillars (*Euphydryas phaeton* Drury: Nymphalidae) and their parasitoids, as an example of interactions of aggregated lepidopteran hosts and specialist parasitoids. This system is particularly suitable for examining

host-parasitoid interactions in natural populations because: 1) the egg clusters of *E. phaeton* are easily located, 2) caterpillars construct communal webs at the tops of host plant stalks, which are about 1 m in height, making them easy to monitor and manipulate, 3) parasitoids are common and large enough that they can be observed easily at the webs and 4) activity of hosts and parasitoids is mainly diurnal. Data from recent studies are incorporated with those of published research to show that these caterpillars defend themselves against their parasitoids and the parasitoids respond accordingly. The second objective here is to compare the *E. phaeton*-parasitoid pattern with other *Euphydryas* host-parasitoid systems. This comparison indicates the constraints on these host-parasitoid interactions as a consequence of climatic factors.

The Host-Parasitoid System

E. phaeton and its parasitoids were studied at the Conservation Center at Front Royal, Virginia, from 1977 through 1981. The Baltimore checkerspots deposited eggs in clusters of about 274 (Stamp, 1982a) in June on their larval host plant turtlehead (*Chelone glabra* L.: Scrophulariaceae), which is a perennial that forms clones in wet meadows and along streams. These butterflies tend to lay their eggs with those of other females (Stamp, 1982b). As a consequence of this, coupled with egg loss from predation and parasitism of less than 10%, larval group size varied initially from about 250 to 2500 (Stamp, 1981a, b). The first three instars formed compact communal webs in July, feeding on leaves enclosed within and adjacent to their webs. Larval activity at webs varied through the day and month, with larvae molting synchronously within webs and third instar larvae spending more time outside webs as a consequence of consuming food more rapidly than first instar larvae (Stamp, 1982a). The caterpillars began diapause as fourth instar larvae in webs in early August. In the fall these caterpillars left the webs to overwinter in small groups in the plant litter on the ground (Bowers, 1978; Stamp, 1982a). The late instar larvae fed from April through mid-May and then pupated.

Apanteles euphydryidis Muesebeck (Braconidae) is a specialist larval parasitoid of *E. phaeton*, with only one other recorded host, the closely-related Harris' checkerspot (*Chlosyne harrissii*, Marsh, 1979). These wasps attacked the web-making early instar larvae of *E. phaeton* in July through early August.

Female *Apanteles* were found at 20-50% of the early instar webs (Stamp, 1982c). The wasps' attendance of the webs varied through the day, with the highest numbers of *Apanteles* searching the surface of the webs in late morning and early afternoon. Webs were attended as early as 0600 and as late as 2100, which suggests that the parasitoids remained at the webs overnight.

The parasitoids attended the webs for hours at a time, with a third of

each hour spent searching for hosts (Stamp, 1982c). When *Apanteles* on the outside of the webs located caterpillars inside the webs, they palpitated the web surface with their antennae, often turning in circles, and probed that area with their ovipositors. Usually, the parasitoids attacked the caterpillars by thrusting their ovipositors through the webbing and, if close enough, into caterpillars for a few seconds. *Apanteles* wasps also attacked larvae when they were outside the webs but considerably less often. Here a wasp carefully approached a larva from behind and thrust the ovipositor forward between her legs into the caterpillar. Generally the wasps avoided caterpillars on the outer surface of the webs, probably as a consequence of the defensive behaviors of caterpillars.

Although 42% of the emerging *Apanteles* were males (Table 1), males seldom occurred at webs (e.g. 2.8% of 142 *Apanteles* observations in 1981). Males emerged a day or two before females and most likely mating occurred at the cocoons. The occasional males at early instar webs created havoc by fanning their wings and walking over larvae to approach females; the caterpillars thrashed vigorously and the females had to retreat until the caterpillars calmed.

The *Apanteles* wasps overwintered as immatures in the diapausing caterpillars. Prediapause caterpillars dissected were parasitized 6% of the time in both 1978 and 1979 (Stamp, 1982c). In the spring the immature parasitoids ate through the cuticle of the hosts, spun cocoons and emerged as adults a week or two later. Solitary *Apanteles* exited from a few larvae in April, but most of the larvae with *Apanteles* cocoons occurred in early May, with 7.5 ($\pm$1.5 SE) parasites per host. Comparison of the means of 2.9 ($\pm$0.4 SE) parasites per diapausing fourth instar larva in August and cocoons per host both in April and May suggests that the solitary parasites emerged earlier in the spring than those aggregated in hosts. The *Apanteles* emerging in the spring attacked the late instars of *E. phaeton*. Their offspring prolonged the last host stage up to eight weeks and emerged in the summer when web-making early instars were available again. Parasitism of sixth instars prior to the adult flight period was 20% in 1979 but may vary considerably among years.

Benjaminia euphydryadis (Viereck): Ichneumonidae is a specialist larval parasitoid on *E. phaeton*, with only one other recorded host, *Chlosyne harrissii* (Carlson, 1979). These parasitoids attacked the early instars by traveling from web to web, spending less than a minute at each (41 sec $\pm$12 SE, n=5 wasps). They probed the webs, usually inserting the entire abdomen (6 mm in length with the ovipositor) into the webs at several locations. This behavior shook the webs, with many larvae responding by simultaneously and vigorously thrashing for several minutes after the wasps departed (Edwards, 1884; Stamp, 1982c). Parasitism of diapausing fourth instar larvae was 6% and 4% in 1978 and 1979, respectively (Stamp,

Table 1. Summary of patterns of *Apanteles* parasitoids using *Euphydryas* caterpillars.

Host *Euphydryas*	Parasitoid *Apanteles*	Number of Parasitoid Generations	x̄ Parasites/ Larva ± SE (n=hosts)	Host Instar Exited From	Time to Wasp Emergence from Cocoons in Weeks	% Females, with χ^2_c test for Sex Ratio (n=wasps)	Location	Reference
editha	koebelei	1-2	20.4 ±1.7 (40)	late	2	67.5 p<0.001 (815)	Jasper Ridge, Calif.	White, 1973
phaeton	euphydryidis	1-2	1 (80+)	4th	1	—	central Mass.	Bowers, 1979; pers. comm.
		1-2	9.8 ±2.3 (16)	6th	1	67.4 p<0.001 (141)	Manlius, N.Y.	Stamp, unpubl. data
		2 minor	1	4th	1-2	—	Front Royal, Va.	Stamp, 1982c; unpubl. data
		major	7.5 ±1.5 (37)	5th	1-2	—		
		major	28.4 ±2.7 (37)	6th	2	57.9 p<0.001 (561)		
aurinia	bignellii	3 major	2.8 ±0.3 (51)	late 3rd	1	—	Oxford, England	Porter, 1983
		major	3.7 ±0.2 (156)	late 4th	1-2	—		
		major	44.7 ±3.6 (41)	6th	4-7	—		

1980). *Benjaminia*, a solitary parasite, overwintered in its diapausing host. In June the mature parasite caused the cuticle of its host to puff and harden and, thus, serve as a cocoon prior to its emergence two to three weeks later.

Defense by Caterpillars and Response by Parasitoids

Often the caterpillars defended themselves from attack by parasitoids, usually by thrashing the front half of the body back and forth and occasionally knocking away wasps (Stamp, 1982c). When numerous *E. phaeton* larvae occurred in one location on webs, disturbance by parasitoids resulted in simultaneous thrashing by caterpillars. This defensive behavior lasted up to 15 min with wasps moving to unoccupied portions of the web or adjacent leaves, and many larvae moving from that area of the web. The caterpillars also defended themselves by reaching around and attempting to contact the parasitoids and regurgitate on them. The *Apanteles* wasps spent considerable time grooming after contact with defensive caterpillars.

The effect of tactile disturbance of larvae was examined in the laboratory. Stalks of turtlehead with communal webs were collected and kept in water, with fresh stalks added daily. For both second and third instars, 60 larvae were observed for one minute each to determine the behavior of undisturbed caterpillars. Then each of these 60 larvae was touched with a two-haired brush (simulating the touch of an *Apanteles* wasp palpitating with its antennae). In response to this tactile stimulation, the larval instars displayed an array of escape and defensive behaviors (Fig. 1). Third instar larvae were more likely to thrash than second instar larvae. This may reflect the body size ratio of caterpillars to their major natural enemies. For example, *Apanteles* wasps were larger than the first instar larvae, but second instar larvae were two times the size of *Apanteles* and the third instar larvae four times that of *Apanteles*. Thrashing by third instar larvae was more effective against the wasps than that by the smaller instars because third instars were more likely to knock the wasps away. In contrast, larvae of similar size to the wasps may be more effective in using regurgitation as a deterrent against these wasps than by trying to knock them away. These larvae were more likely to make immediate contact and smear regurgitate on their attackers than were caterpillars much larger than the wasps.

I also disturbed larvae in the field, but this time instead of directly stimulating larvae, each web was jabbed 10 times with a dissecting needle to create a general web disturbance, simulating that caused by *Benjaminia* wasps. For both first and third instar webs, larvae moved into the webs within three minutes after the disturbance (Fig. 2). The first instar larvae increased their thrashing significantly, whereas the third instar larvae decreased their head-jerking. Again, this difference may reflect the body size ratio of caterpillars to their insect enemies. First instar larvae may
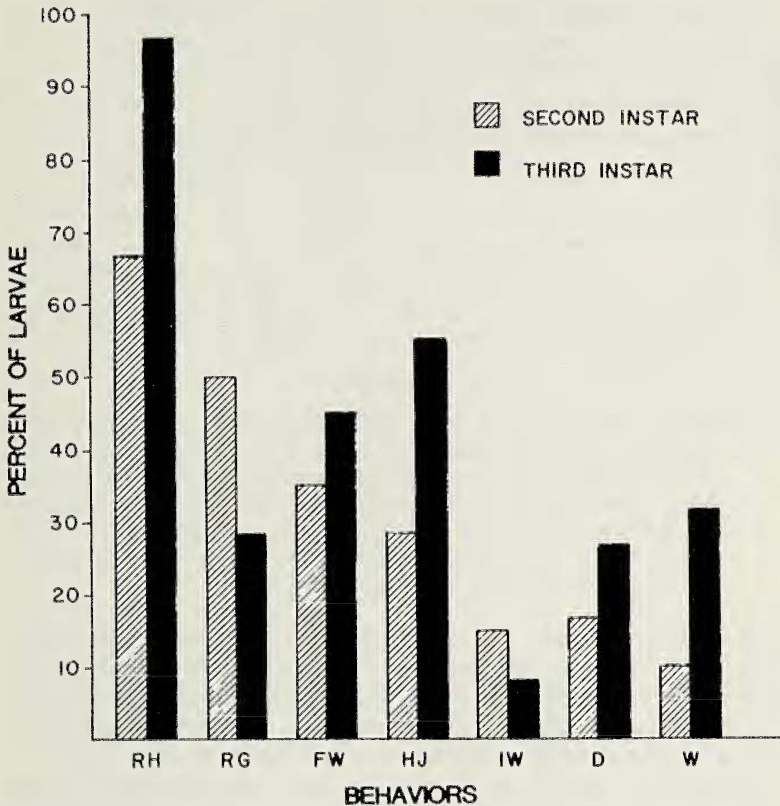
Fig. 1. Escape and defensive behaviors of *E. phaeton* larvae exhibited in the laboratory. Caterpillars were disturbed by a two-haired brush, simulating the touch of an *Apanteles* wasp. RH - reared head, RG - regurgitated, FW - walked away quickly, HJ - head-jerking, IW - into web, D - dropped from web and W - wriggled (all legs detached). Third instar larvae thrashed more than second instar larvae (χ^2_c text, $p < 0.05$). Before disturbance (not shown), none of the third instar larvae exhibited escape or defensive behaviors and second instar larvae spent less than 1% of their time in such behaviors.

benefit by reacting together to any disturbance, except when touched directly. In this case, when larvae can be easily overwhelmed by their insect enemies, catalepsis may be a more prudent behavior than thrashing (e.g. Rotheray, 1981). For instance, larval movement may trigger oviposition behavior by parasitoids (Vinson, 1976). Also, predatory pentatomids were more likely to encounter active tent caterpillars (*Malacosoma californicum*) than inactive ones (Iwao & Wellington, 1970a). *E. phaeton*
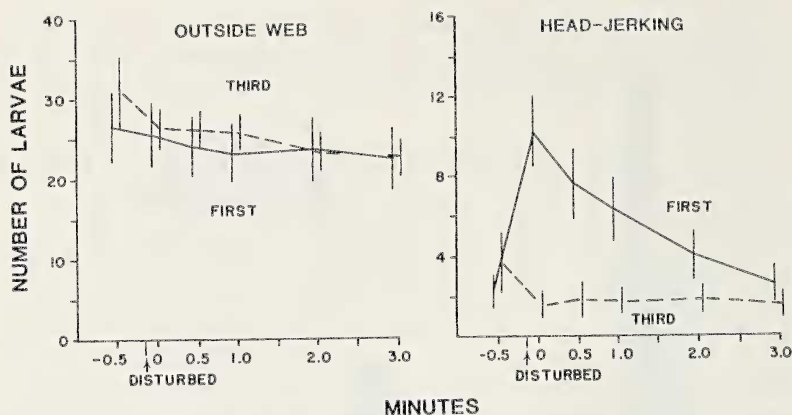
Fig. 2. Response by *E. phaeton* larvae under field conditions to general web disturbance, simulating that caused by *Benjaminia* wasps. Solid lines indicate first instar larvae, whereas dashed lines show third instar larvae. Bars indicate ± one standard error. Number of larvae outside of webs before and after disturbance are shown (Wilcoxon paired-sample tests with n=20, p<0.001) as are number of larvae head-jerking before and after disturbance (p<0.001).

third instar larvae were more likely to defend themselves effectively against insect enemies than were first instar larvae. Consequently, third instar larvae may spend more time feeding and less energy on defense by reacting to offensive tactile stimuli rather than to a general array of stimuli, such as shadow and web disturbance, as the first instar larvae do.

In addition to differences in defensive behaviors among instars, the instars varied in terms of potential defensive structures on their bodies. First instar larvae had sparse setae, whereas second through sixth instar larvae had rows of tubercles with spines radiating at 45° angles. By the third instar, the combination of tubercle and spines was similar in length to that of the ovipositor of the *Apanteles* parasitoids and, thus, may have deterred penetration of the ovipositor as well as serve as sensory devices (Table 2). Ayre and Hitchon (1968) found differences in the setae covering tent caterpillar instars (*Malacosoma americanum*), with ants unable to attack densely-haired late instars successfully. Thus, such body structures may be effective defensively when the body size ratio of caterpillar to insect enemy is relatively large (e.g. greater than two).

To examine the interactions of checkerspot caterpillars and the parasitoid *Apanteles euphydryidis*, 20 wasps were observed at first instar webs in the field and six each, at second and third instar webs. Comparison of the prediapause instars indicated that *Apanteles* wasps encountered these larvae outside the webs at a similar rate (Fig. 3). However, the wasps seldom attacked first and second instar larvae outside the webs (less than

Table 2. Comparison of the lengths of potential sensory and defensive structures on *E. phaeton* larvae to ovipositor lengths of *Apanteles euphydryidis*. The tubercle-spine length of the third instar larvae was similar to the ovipositor length of the wasps and the tubercle-spine length of fourth instar larvae was greater than the ovipositor length (Stamp, 1982c).

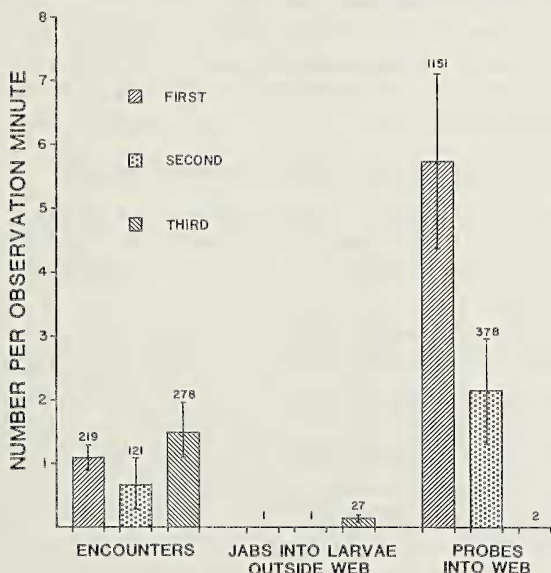| | Setae of first instar | Tubercle-spine of | | | Wasp ovipositor |
		second	third instars	fourth	
$\bar{x}$ length in mm	0.16	0.29	0.78	1.00	0.76
SE	0.01	0.02	0.01	0.02	0.01
n	30	30	30	33	30

Fig. 3. Interactions of *E. phaeton* larvae and *Apanteles euphydryidis* in natural populations. Responses by parasitoids at webs of first, second and third instar larvae are show. Bars indicate ± one standard error and numbers show total parasitoid observations per category. "Encounters" are between parasitoids and caterpillars on the outside of webs and were similar among instars (Kruskal-Wallis text, v=2, p>0.05). Jabs into larvae outside webs and probes into webs varied among instars (Kruskal-Wallis tests, p<0.01).

1% of the encounters) but often jabbed at third instar larvae there (10% of encounters). In contrast, the wasps probed most at first instar webs and least at webs of third instars. These differences in response by the wasps to the caterpillars suggest again that defensive behaviors varied among the host instars.

Some *E. phaeton* larvae tried to escape when disturbed, by crawling away quickly, often into the web, or by dropping from the web, usually on a silk thread (Fig. 1). To determine how webs might protect larvae from parasitism, I damaged webs by making small holes in them and then monitored activities of caterpillars and parasitoids (Stamp, 1981a). Larvae in the outer portion of the damaged webs exited from the webs and joined those larvae on the outside of the webs. Damaged webs were repaired, usually within 24 hours. But parasitoid access to larvae by damaging the webs did not increase the level of parasitism. In fact, fewer parasitoids were found at the damaged webs compared to undamaged webs. It appears that the parasitoids did better when they could attack larvae through the webbing, and perhaps avoid the defensive responses of larvae. Most likely webs were important, at least relative to these parasitoids, when the larvae were molting. At that time the caterpillars were deep within the webs, usually surrounded by frass and layers of webbing. In large webs, molting caterpillars were out of reach of both the major larval parasitoids.

Example of an Aggregated Host-Parasitoid System

These studies show that *E. phaeton* caterpillars exhibit a variety of escape and defensive behaviors, these behaviors vary among instars and *Apanteles* parasitoids respond accordingly. In addition to behavioral differences among instars, molting caterpillars are less defensive than active caterpillars and molt synchronously in the core of the web. This suggests that the number of available, non-parasitized caterpillars per web may fluctuate sharply, with periods of relatively few available individuals at a web alternating with periods of abundant hosts (Stamp, 1982d). Attendance of webs by parasitoids should reflect this fluctuation in host availability, with webs of molting caterpillars unattended by *Apanteles*. Some indirect evidence, that *Apanteles* wasps were moving among webs more frequently than expected (Stamp, 1982d), supports this contention. In contrast, *Benjaminia* wasps which are larger and reach farther into webs than *Apanteles* may be less constrained by such changes in host availability.

Many aggregated host species exhibit defensive behaviors and fluctuating numbers of available hosts, due to molting in protected locations and perhaps latter instars defending themselves more effectively than early instars. For example, Iwao and Wellington (1970b) found that tent caterpillars differed in their behavior, with inactive types less defensive and parasitized more frequently. Active fifth instar larvae were generally

aggressive enough to ward off predatory pentatomids, whereas other, smaller instars were not (Iwao & Wellington, 1970a). Other lepidopteran species have been reported defending themselves effectively against insect enemies (Smith *et al.*, 1955; Morris, 1963). Therefore, such host-parasitoid systems may be similar to that of *E. phaeton*, with parasitoids responding to host patches in terms of the numbers of available hosts rather than absolute numbers of hosts and exhibiting different attack behaviors relative to host instar and activity.

E. phaeton larvae are similar to some other aggregated lepidopteran species in that they overwinter as mid-instars. Consequently, vulnerable larvae are available during two distinct periods, even though this species is univoltine (Fig. 4). Caterpillars are present for about five weeks in the summer and four to six weeks in the spring, with a gap of four to six weeks between late and early instars in early summer (during pupation and adult flight period; Bowers, 1979; Stamp, 1982c).

One parasitoid attacks hosts at these two larval periods whereas the other does not. The *Apanteles* wasps have a generation at each larval host period, which is regulated by their laying numbers of eggs to suit the size of larval stages involved. In contrast, the *Benjaminia* parasitoids have one generation per that of the host. *Benjaminia* are four times the length of *Apanteles*. Consequently, *Benjaminia* immature parasites require more food than a single *Apanteles* and thus they must complete their development in a later instar. This contrast in solitary versus gregarious
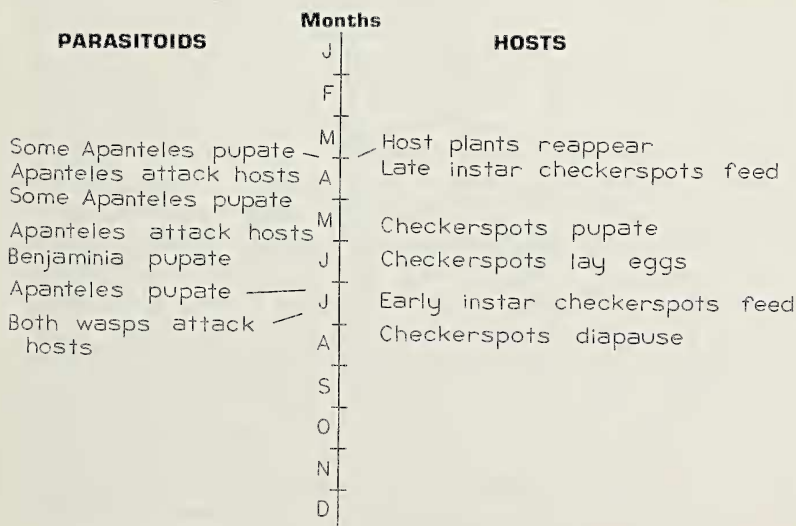

Fig. 4. Association of checkerspots (*Euphydryas phaeton*) and larval parasitoids (*Apanteles euphydryidis* and *Benjaminia euphydryadis*) in Virginia.

development by the parasites, by contributing more parasites per host and an additional generation per that of the host, should yield a larger population of *Apanteles* than *Benjaminia* in the summer. Based on the mean numbers of *Apanteles* cocoons per host per parasitoid generation in Table 1, with 57.9% of them females and 50% of those killed by hyperparasitoids (parasitoids of parasitioids; Stamp, 1981c), the number of female *Apanteles* should have been 94 times that of *Benjaminia*. Observations at webs were 100 female *Apanteles* wasps to one *Benjaminia* in July 1979 (Stamp, 1982c). That the levels of parasitism for the early instars were the same for these two parasitoids in that year when the adult numbers differed so suggests that individual *Benjaminia* may be more efficient at exploiting the host population than are individual *Apanteles*. Thus, the *Benjaminia* pattern (a solitary, large parasite per host, with one generation per that of the host) and the *Apanteles* pattern (adjustment of parasitoid numbers relative to host size with multiple generations per that of the host) illustrate a tradeoff in parasitoid packaging. This is analogous to the alternative strategies in plants, of producing either a few, large, competitive seeds or numerous, small, colonizing propagules (Harper *et al.*, 1970).

Comparison of *Euphydryas* Host-Parasitoid Systems

Euphydryas species are attacked by one to three larval parasitoids, often by an *Apanteles*, a *Benjaminia* and a tachinid species (Table 3). Generally, egg parasitism has not been reported for *Euphydryas* species, even though eggs remain on host plants for several weeks (e.g. two weeks for *E. editha*, Singer, 1972; three for *E. phaeton*, Stamp, 1981b; three to six for *E. gillettii*, Williams *et al.*, 1983; five for *E. aurinia*, K. Porter, 1981). However, *E. phaeton* egg clusters were parasitized frequently but at a low level by trichogrammatid wasps (Table 3).

Only the *Apanteles* parasitoids exhibited more than one generation per that of the host and this may vary with location (Table 1; and White, 1973). The *Apanteles* species emerged one to two weeks after spinning cocoons, except in *Apanteles bignellii* on sixth instar *E. aurinia*. Here the fully formed wasps remained in their cocoons from four to seven weeks, emerging when newly-hatched hosts were available again (Porter, 1983). In contrast, apparently the other *Apanteles* species prolonged the last host instar and then spun cocoons just prior to the availability of early instar hosts (e.g. Stamp, 1981c). The sex ratio of the emerging wasps was skewed towards females (Table 1). As newly-emerged females were likely to be mated at cocoons, fewer males may have been necessary to insure fertile (female) eggs (White, 1973). Thus, a female could increase her fitness by laying more female eggs than male ones.

The variation in parasitism among years for *Euphydryas* species was considerable (Table 3). Parasitism was cited as the major factor in marked

Table 3. Sets of parasitoids attacking *Euphydryas* species, with some indication of parasitism levels.

Host *Euphydryas*	Parasitoid Species	Level of Parasitism	Location	Reference
aurinia	*Apanteles bignellii* (Braconidae)	1-4% late 3rd instar 14% late 4th instar 8-75% 6th instar	Oxford, England	Porter, 1983
	Apanteles melitaearum	—	northern England	K. Porter, pers. comm.
	Erycia cinerea (Tachinidae)	—	England	
chalcedona	*Apanteles koebelei*	—	western U.S.A.	Marsh, 1979
	Benjaminia fuscipennis (Ichneumonidae)	—	western U.S.A.	Carlson, 1979
	Siphosturmia melitaeae (Tachinidae)	—	Jasper Ridge, CA	Brown and Ehrlich, 1980
editha	*Apanteles koebelei*	2-61% late instars	Jasper Ridge, CA	Ehrlich, 1965
		0-67% late instars	numerous sites in	White, 1973
	Benjaminia fuscipennis	0-25%	Calif. and Oregon	
	Siphosturmia melitaeae	0-27%		
gillettii	*Benjaminia fuscipennis**	30%	Park Co., WY	E. H. Williams, pers. comm.
	Peromalus vanessae (Pteromalidae)	—	Gunnison Co., CO	Williams et al., 1983
phaeton	trichogrammatid wasp	5%	Front Royal, VA	Stamp, 1981b
	Apanteles euphydryidis	6% early instars 20% late instars		Stamp, 1982c
	Benjaminia euphydryadis	4-6%		Stamp, 1980
	Peromalus puparum	—	northeastern	Stamp, unpubl. data
	Compsilura concinnata (Tachinidae)	—	U.S.A	Arnaud, 1978

*identified tentatively by the author, based on Cushman (1933).

population fluctuations of *E. aurinia* (Ford and Ford, 1930; Porter, 1983), but it was not an important factor in population fluctuations of *E. editha* and *E. chalcedona* (Ehrlich *et al.*, 1975; Lincoln *et al.*, 1982).

This difference may reflect constraints on host-parasitoid interactions by climatic factors. In *Euphydryas* species of the western United States, these fluctuations have been attributed to the distribution, abundance and health of the host plants, which are affected severely by drought (Ehrlich *et al.*, 1980; Mooney *et al.*, 1980). For example, up to 99% of *E. editha* using *Plantago erecta* died from starvation before reaching diapause as a consequence of host plant senescence (Singer, 1972; White, 1974). Thus, larvae from eggs laid late in the spring were less likely to obtain enough food before diapause than those from eggs deposited earlier. This suggests that the parasitoids may benefit by attacking early instars when they first become available rather than throughout the spring season (White, 1973). However, with the presence of early instars as short as three weeks in duration (Singer, 1972), such synchrony by the parasitoids with their hosts (essentially with the first half of that period) may be difficult. Some evidence indicates that diapausing larvae previously parasitized by *Apanteles* are less likely to survive than nonparasitized ones (White, 1973). If few parasitized larvae survive over the diapause period, the *Apanteles* population the following spring relative to that of the host should be small.

The interactions of parasitoids and *E. gillettii* in the Beartooth Mountains of Wyoming may provide another example of limitations imposed by climatic factors. *E. gillettii* eggs hatch between early August and mid-September, but larvae hatching in September die due to the onset of winter (i.e. frosts, snow and leaf abscission of host plants, Williams, 1981). Again, the parasitoids (in this case *Benjaminia*) may benefit by synchrony of adult emergence with caterpillars hatching in August, as opposed to September. This population of *E. gillettii* larvae undergo two winters before reaching maturity (Williams *et al.*, 1983) and consequently *Benjaminia* also require two years for development (E. H. Williams, pers. comm.). The first and second instars of *E. gillettii* are available for three to four weeks (in early September), third and fourth instars for about seven weeks (late May to mid-July of the second summer) and fifth and sixth instars for four to five weeks (late May to early July in the followng year; E. H. Williams, pers. comm.). This would seem to provide ample opportunity for attack by *Apanteles*, but such parasitoids have not been found using *E. gillettii*. Perhaps the combination of a short, variable period (three to four weeks) to attack the young instars and difficulty in surviving the diapause period imposes too severe a constraint for *Apanteles* populations to use this host successfully.

Drastic fluctuations in *E. phaeton* have been noted (Bowers, 1979; Clench, 1979). Fluctuations in Baltimore checkerspot numbers have been linked to periodic flooding and presumably drowning or washing away of

caterpillars (Brussard and Vawter, 1975). In addition, defoliation of the host plants by sawfly larvae (*Macrophya nigra* and *Tenthredo grandis*: Tenthredinidae) when *E. phaeton* prediapause larvae were also feeding may contribute to high mortality of checkerspots (Stamp, unpubl. data). But flooding and defoliation probably affect parasitized and nonparasitized larvae (and consequently numbers of adult hosts and parasitoids) similarly. Furthermore, parasitism is unlikely to contribute to population fluctuations of *E. phaeton* when attack by generalist hyperparasitoids on both generations of *Apanteles* is high, as it was in Virginia (43-57% killed, Stamp, 1981c).

In contrast, climatic factors in the spring may influence host-parasitoid interactions of *E. phaeton* in the same way that they affect *E. aurinia*, a European checkerspot that uses habitats similar to those of *E. phaeton*. When air temperatures on average were low and skies clear, *E. aurinia* postdiapause larvae fed at an optimal rate, by using basking behavior to become independent of ambient temperatures (Porter, 1982). Under these conditions, *Apanteles* emerged as adults after a prolonged pupal period and when most of their hosts had already pupated (Porter, 1983). For instance, when parasitoid emergence occurred in synchrony with host availability, 75% of the postdiapause larvae were parasitized, whereas when emergence was asynchronous, the level of parasitism was only 8%. The period when larvae are present for *Apanteles* adults in the spring may be as short as a few days in some years (Porter, 1983). *E. phaeton* postdiapause larvae are subject to variable spring conditions also and exhibit basking behavior (Stamp, pers. observ.).

The major difference between these two host-parasitoid systems is that the prediapause larvae of *E. aurinia* are present for the parasitoids up to eight weeks in contrast to five weeks for those of *E. phaeton* (Porter, 1981; Stamp, 1982c). As a consequence, some *Apanteles* on *E. aurinia* reach maturity and produce cocoons in late summer, on late second and late third instars (Porter, 1983). These wasps then attack the larvae of that summer, which contributes a partial generation of *Apanteles* that does not occur in the *E. phaeton* system. Therefore, with relatively more parasitoids emerging from and then attacking hosts in the spring, especially if the climatic conditions favor host-parasitoid synchrony, parasitism of *E. aurinia* late instars may reach extremely high levels. Parasitism may cause dramatic declines in the host population, particularly if high levels of parasitism occur over consecutive years. Here the fluctuations in parasitism should correspond with the climatic patterns of spring and summer, which determine the length of the larval periods at those times.

Literature Cited

ARNAUD, P. H., JR., 1978. A host-parasite catalog of North American Tachinidae (Diptera). U.S.D.A. Misc. Publ. No. 1319. Washington, D.C. 860 p.

AYRE, G. L. & D. E. HITCHON, 1968. The predation of tent caterpillars, *Malacosoma americana* (Lepidoptera: Lasiocampidae) by ants (Hymenoptera: Formicidae). Can. Ent. 100:823-826.

BOWERS, M. D., 1978. Overwintering behavior in *Euphydryas phaeton* (Nymphalidae). J. Lepid. Soc. 32:282-288.

_____, 1979. Unpalatability as a defense strategy of checkerspot butterflies with special reference to *Euphydryas phaeton* (Nymphalidae). Ph.D. Diss., Univ. of Mass.

BROWN, I. L. & P. R. EHRLICH, 1980. Population biology of the checkerspot butterfly, *Euphydryas chalcedona*: structure of the Jasper Ridge colony. Oecologia 47: 239-251.

BRUSSARD, P. F. & A. T. VAWTER, 1975. Population structure, gene flow and natural selection in populations of *Euphydryas phaeton*. Heredity 34:407-415.

CARLSON, R. W., 1979. Ichneumonidae, pp. 315-740. *In* K. V. Krombein, P. D. Hurd, Jr., D. R. Smith and B. D. Burk (eds.) Catalog of Hymenoptera in America north of Mexico, Vol. 1. Symphyta and Apocrita (Parasitica). Smithsonian Institution, Washington, D.C.

CLENCH, H. K., 1979. How to make regional lists of butterflies: some thoughts. J. Lepid. Soc. 33:216-231.

CUSHMAN, R. A., 1933. Descriptions of new ichneumon-flies, with taxonomic notes. Proc. U.S. Natl. Mus. 82, Art. 14, 16 p.

EDWARDS, W. H., 1884. The butterflies of North America. Vol. II. Houghton, Mifflin, Boston. 331 p.

EHRLICH, P. R., 1965. The population biology of the butterfly, *Euphydryas editha*. II. The structure of the Jasper Ridge colony. Evolution 19:327-336.

EHRLICH, P. R., D. D. MURPHY, M. C. SINGER, C. B. SHERWOOD, R. R. WHITE & I. L. BROWN, 1980. Extinction, reduction, stability and increase: the responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. Oecologia 46: 101-105.

EHRLICH, P. R., R. R. WHITE, M. C. SINGER, S. W. McKECHNIE & L. E. GILBERT, 1975. Checkerspot butterflies: a historical perspective. Science 188:221-228.

FORD, H. D. & E. B. FORD, 1930. Fluctuations in numbers, its influence on variation, in *Melitaea aurinia*, Rott. (Lepidoptera). Trans. Entomol. Soc. Lond. 78:345-351.

HARPER, J. L., P. H. LOVELL & K. G. MOORE, 1970. The shapes and sizes of seeds. Annu. Rev. Ecol. Syst. 1:327-356.

IWAO, S. & W. G. WELLINGTON, 1970a. The influence of behavioral differences among tent-caterpillar larvae on predation by a pentatomid bug. Can. J. Zool. 48:896-898.

—————————, 1970b. The western tent caterpillar: qualitative differences and the action of natural enemies. Res. Popul. Ecol. 12:81-99.

LINCOLN, D. E., T. S. NEWTON, P. R. EHRLICH & K. S. WILLIAMS, 1982. Coevolution of the checkerspot butterfly *Euphydryas chalcedona* and its larval food plant *Diplacus aurantiacus*: larval response to protein and leaf resin. Oecologia 52:216-223.

MARSH, P. M., 1979. Braconidae, pp. 144-295. *In* K. V. Krombein, P. D. Hurd, Jr., D. R. Smith and B. D. Burk (eds.) Catalog of Hymenoptera in America north of Mexico, Vol. 1. Symphyta and Apocrita (Parasitica). Smithsonian Institution, Washington, D. C.

MATTHEWS, R. W., 1974. Biology of Braconidae. Annu. Rev. Ent. 19:15-32.

MOONEY, H. A., P. R. EHRLICH, D. E. LINCOLN & K. S. WILLIAMS, 1980. Environmental controls on the seasonality of a drought deciduous shrub, *Diplacus aurantiacus* and its predator, the checkerspot butterfly, *Euphydryas chalcedona*. Oecologia 45:143-146.

MORRIS, R. F., 1963. The effect of predator age and prey defense on the functional response of *Podisus maculiventris* Say to the density of *Hyphantria cunea* Drury. Can. Ent. 95:1009-1020.

MORRISON, G. & D. R. STRONG, JR., 1980. Spatial variation in host density and the intensity of parasitism: some empirical examples. Environ. Ent. 9:149-152.

PORTER, K., 1981. The population dynamics of small colonies of the butterfly *Euphydryas aurinia*. Ph.D. Diss., Oxford Univ.

—————————, 1982. Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. Oikos 38:308-312.

PORTER, K., 1983. Multivoltinism in *Apanteles bignellii* and the influence of weather on synchronisation with its host *Euphydryas aurinia*. Ent. exp. appl. 34:155-162.

ROTHERAY, G. E., 1981. Host searching and oviposition behaviour of some parasitoids of aphidophagous Syrphidae. Ecol. Ent. 6:79-87.

SINGER, M. C., 1972. Complex components of habitat suitability within a butterfly colony. Science 176:75-77.

SMITH, O. J., P. H. DUNN & J. H. ROSENBERGER, 1955. Morphology and biology of *Sturmia harrisinae* Coquillet (Diptera), a parasite of the western grape leaf skeletonizer. Univ. Calif. Publ. Ent. 10:321-358.

STAMP, N. E., 1980. Effect of group size on an egg-clustering butterfly. Ph.D. Diss., Univ. of Maryland.

—————————, 1981a. Effect of group size on parasitism in a natural population of the Baltimore checkerspot *Euphydryas phaeton*. Oecologia 49:201-206.

—————————, 1981b. Parasitism of single and multiple egg clusters of *Euphydryas phaeton* (Nymphalidae). J. N. Y. Ent. Soc. 89:89-97.

—————————, 1981c. Behavior of parasitized aposematic caterpillars: advantageous to the parasitoid or the host? Am. Nat. 118:715-725.

—————————, 1982a. Aggregation behavior in Baltimore checkerspot caterpillars *Euphydryas phaeton* (Nymphalidae). J. Lepid. Soc. 36:31-41.

—————————, 1982b. Selection of oviposition sites by the Baltimore checkerspot, *Euphydryas phaeton* (Nymphalidae). J. Lepid. Soc. 36:290-302.

—————————, 1982c. Behavioral interactions of parasitoids and Baltimore checkerspot caterpillars (*Euphydryas phaeton*). Environ. Ent. 11:100-104.

_____, 1982d. Searching behaviour of parasitoids for web-making caterpillars: a test of optimal searching theory. J. Anim. Ecol. 52:387-395.

VINSON, S. B., 1976. Host selection by insect parasitoids. Annu. Rev. Ent. 21:109-133.

WHITE, R. R., 1973. Community relationships of the butterfly, *Euphydryas editha*. Ph.D. Diss. Stanford Univ.

_____, 1974. Food plant defoliation and larval starvation of *Euphydryas editha*. Oecologia 14:307-315.

WILLIAMS, E. H., 1981. Thermal influences on oviposition in the montane butterfly *Euphydryas gillettii*. Oecologia 50:342-346.

WILLIAMS, E. H., C. E. HOLDREN & P. R. EHRLICH, 1983. The life history and ecology of *Euphydryas gillettii* Barnes (Nymphalidae). J. Lepid. Soc.: in press.